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REPRODUCTION IN TWO SYMPATRIC SPECIES OF *MACOMA* (BIVALVIA)

JOHN GIBSON RAE III[1]

Pacific Marine Station, University of the Pacific, Dillon Beach, California 94929

The phenomenon of sexual differentiation in molluscs has been well reviewed (Coe, 1936, 1940, 1943a). Although a great deal of work has been done on gonadal development in Lamellibranchs, most of it concentrates in seven families: Pectinidae (Sastry, 1963); Teredinidae (Coe, 1943b); Veneridae (Ansell, 1961); Ostreidae (Dinamani, 1974); Mytilidae (Bartlett, 1972); Myacidae (Pfitzenmayer, 1962); and Mactridae (Machell and DeMartini, 1971). The only member of the Tellinidae studied to date is *Macoma balthica* (Lammens, 1967; Caddy, 1967).

Macoma secta (Conrad, 1837) and *M. nasuta* (Conrad, 1837) are geographically sympatric species of the bivalve family Tellinidae. *M. secta* occurs in intertidal sand flats to sediment depths of 60 cm from Vancouver Island, British Columbia, to Bahia Magdalena, Baja California; while *M. nasuta* occurs in muddier substrates intertidally to sediment depths of 40 cm from Kodiak Island, Alaska, to Cabo San Lucas, Baja California (Coan, 1971). Ricketts, Calvin, and Hedgpeth (1969) list *M. secta* as occurring in the Middle Intertidal Zone and *M. nasuta* in the Low Tide Horizon. They are found in decreasing numbers to 25 fathoms (Abbott, 1954). *M. secta* and *M. nasuta* are the characteristic species of the *Macoma* community on the west coast of North America. Thorson (1966) had identified five *Macoma* communities worldwide.

In the present study the seasonal gonadal changes and sex ratios of *Macoma secta* and *M. nasuta* are reported as well as the physical and biotic factors which may influence them. This includes complete qualitative descriptions of the stages of gametogenesis. The reproduction of these species is compared and the reproductive advantage each species has to its particular milieu is examined. Of particular interest is the comparison of the two populations studied, viewing the effectiveness of reproductive barriers. There exists no physical barrier between these sympatric populations. Therefore, crossing must be prevented through environmental and/or physiological barriers.

Materials and Methods

Macoma secta and *M. nasuta* occur sympatrically on Lawson's Flat, a sandy intertidal area, located 0.8 mile from the mouth of Tomales Bay, California. From March 2, 1974, to March 31, 1975, fifteen clams of each species were collected bi-weekly at each spring low tide. An effort was made to select clams from their respective tidal midranges in order to avoid animals living in stress. The midranges for *M. secta* and *M. nasuta* are 45 and 15 cm above mean low water, respectively.

[1] Present address: Department of Zoology and Microbiology, Ohio University, Athens, Ohio 45701.

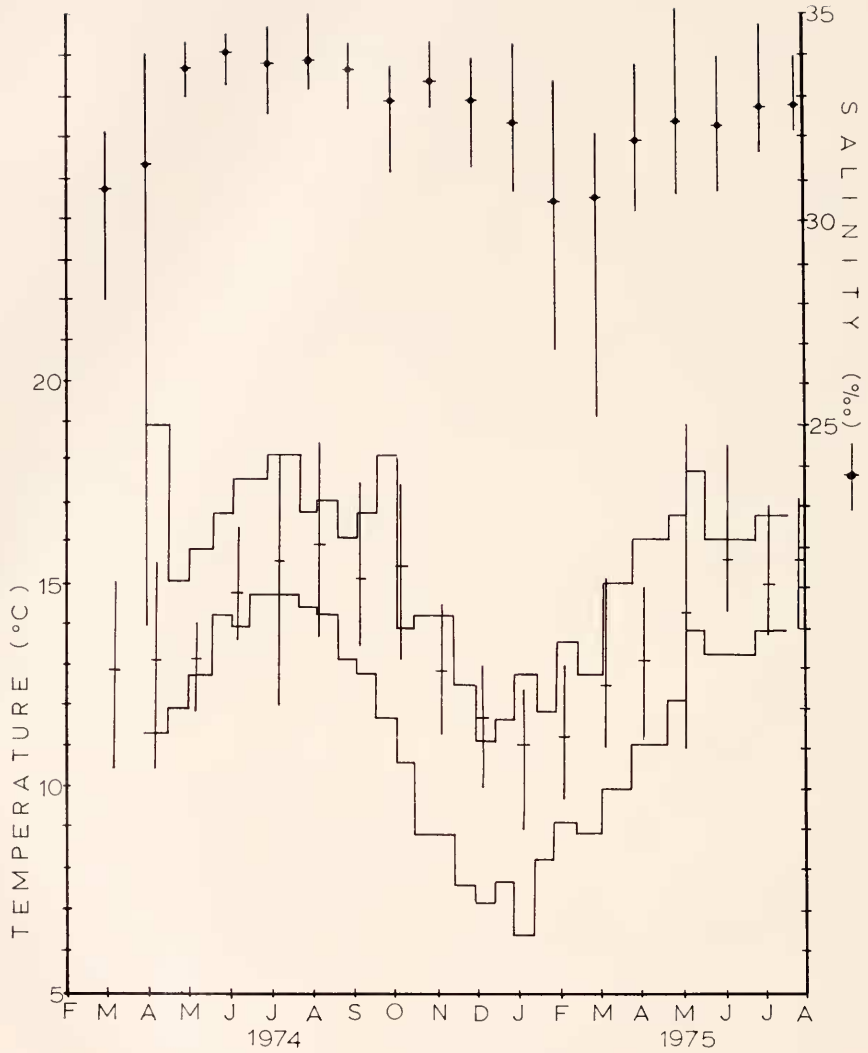

FIGURE 1. Pacific Marine Station weather station data: sea water temperatures and salinities; monthly means and ranges. Superimposed are interstitial maximum-minimum temperatures, taken at 40 cm depth at +60 cm tidal height.

A maximum-minimum thermometer was placed in the sediment to a depth of 40 cm at a tidal height of 60 cm and read bi-weekly. Sea water temperature and salinity were recorded daily at Pacific Marine Station one mile from the Lawson's flat site and are presented in Figure 1.

After collection, the clams were placed in flowing sea water pumped directly from the Pacific Ocean; consequently, the possibility of thermal shock causing gamete release was minimal. They were kept for one day to cleanse the alimentary

tract of most ingested sand. Because of the weakly-developed adductor muscles in *M. secta,* the animals tend to gape and become moribund when left out of the sediment. As a counter measure, rubber bands were used to hold the valves together. This measure was not necessary for *M. nasuta* which has strong adductor muscles. The clams were assigned a number and measured for length and width using vernier calipers. The presence of commensals was noted.

The visceral mass was cut on a transverse axis at a point below the attachment of gills and palps. The lower (ventral) portion was preserved in Bouin's fixative for 24 hours. A 4 mm subsample was dissected and processed by standard histological technique. The tissue was dehydrated with isopropanol, cleared with toluene and embedded with 56 to 58° C paraffin. Sections were cut at 8 to 10 μ, stained progressively with a modification of Harris' hematoxylin (Galigher and Kozloff, 1971, p. 352) and counterstained with Eosin Y.

In studying the seasonal gametogenic cycle, only adults were used. Mature clams with fully differentiated gonads were encountered at sizes above 3.0 cm for *M. secta* and 2.4 cm for *M. nasuta.* Primordial gonadal development was not studied for protandry. Caddy (1967) illustrated the external appearance of the visceral mass of *Macoma balthica* as it passed through the gametogenic cycle. Descriptions for *M. secta* and *M. nasuta* are identical to *M. balthica;* therefore, they are not repeated.

Histological examination of the gonads in *Macoma* allowed the seasonal gonadal cycle to be broken into six stages: inactive; early active; late active; ripe; partially spawned; and spent. This sequence is modified from Ropes and Stickney (1965) for *Mya arenaria.*

Results

Stages of gonadal development for Macoma *and their criteria*

In keeping with Raven's (1961) classification of oogenesis, the term *follicle* is not used here for the basic gonadal developmental unit because *follicular* egg development implies a completely different process from *solitary,* that found in most bivalves. The term *alveolus* is used as described in Ropes and Stickney (1965).

Inactive. The main criterion for this stage is the presence of the contracted alveolus. In *M. nasuta* the vacuolated follicle cells completely fill the alveolus. Sex can usually be determined in males by the presence of residual spermatozoans. It appears the unshed spermatozoa will remain viable over the winter to be shed with the next year's sperm. With females, sex determination is more difficult as residual ova are rarely found. Females in this stage are usually identified by the presence of many noncellular spherical inclusions in the alveoli, which are probably nutritive in function and albuminous in composition. Similar inclusions were described for *Mya arenaria* (Coe and Turner, 1938). Phagocytes are extremely rare in this and other stages. The alveoli have a highly organized appearance in this species and are round and firm.

The general appearance of the gonads of *M. secta* at this stage is characterized by flaccid compressed alveoli in a matrix of disorganized and pycnotic connective

tissue in a state of phagocytosis. The development of vacuolated follicle cells is varied, ranging from none to a thin one cell layer covering the alveolar wall.

Early active. Following the inactive period, gametogenesis is initiated in the early active stage. This is the earliest stage in the next cycle in which the clams can be sexed.

In females of *M. nasuta*, meiosis has produced primary and secondary oogonia and young oocytes have begun to grow out from the alveolar wall. In males, primary and secondary spermatogonia are rapidly being produced, starting to fill in the lumen. Some spermatogonia will be seen throughout the alveolus because they are able to migrate within the matrix of follicle cells. The smaller darkly stained spermatids are usually present towards the center of the lumina. The gonads are more organized as the alveoli anastomize into spaces between muscles and digestive diverticula.

The description of early active for *M. secta* is similar to *M. nasuta* except that phagocytosis is active in *M. secta*, especially in males, resorbing unshed gametes. Also, the male meiotic products of *M. secta* are more closely associated with the alveolar wall, with advanced stages extending into the lumen. This is a result of the poorly developed follicle cells.

Late active. This stage is characterized by a rapid proliferation of gametes. Spermatozoa of both species form streams with their tails extending into the lumen. The arbitrary qualitative maximum limit of spermatozoa present is seventy per cent of the meiotic cells present. In females of both species, oocytes begin to elongate, extending into the lumen on thick stalks. Amphinuclei are evident as they move to the distal end of the oocytes. Very few eggs are mature and most still adhere to the alveolar wall by at least a slender stalk. Young oocytes are present on the wall.

There are a few note worthy differences between species. Male meiotic products are arranged differently. In *M. secta* advancing stages are found increasingly closer to the lumen center. In *M. nasuta* the products are forced into crevasses between the follicle cells resulting in a patchy appearance. Also, the follicle cells of *M. nasuta* decrease in number as gametes are produced. Lastly, the female spherical bodies of *M. nasuta* continually shrink, both in size and number.

Ripe. All clams in this stage are physiologically prepared to spawn. For males of both species, most of the lumen is filled with spermatozoa; qualitatively, the arbitrary minimum of spermatozoa is 70% of all alveolar cells. The sperm form long streams extending into the lumen, with their tails directed toward the center. The first stages of gametogenesis become less evident. For females, almost every oocyte is mature and oval shaped, free in the lumen. A few are still attached by slender stalks to the alveolus wall. Young oocytes are absent from the alveolar walls. Unspawned oocytes of *M. secta* average 51.7 μ with a range of 46 to 57 μ, while oocytes of *M. nasuta* ranged from 48 to 57 μ with a mean of 52.6 μ.

Partially spawned. In this stage there are obvious gaps in the lumina indicating that some gametes have been shed. Most remaining gametes are mature. In both sexes, there is little or no early gametogenic activity.

This ephemeral stage in *M. nasuta* is rarely witnessed. Follicle cells begin to grow on the basal membrane of the alveolus. Individuals appear to spawn in a

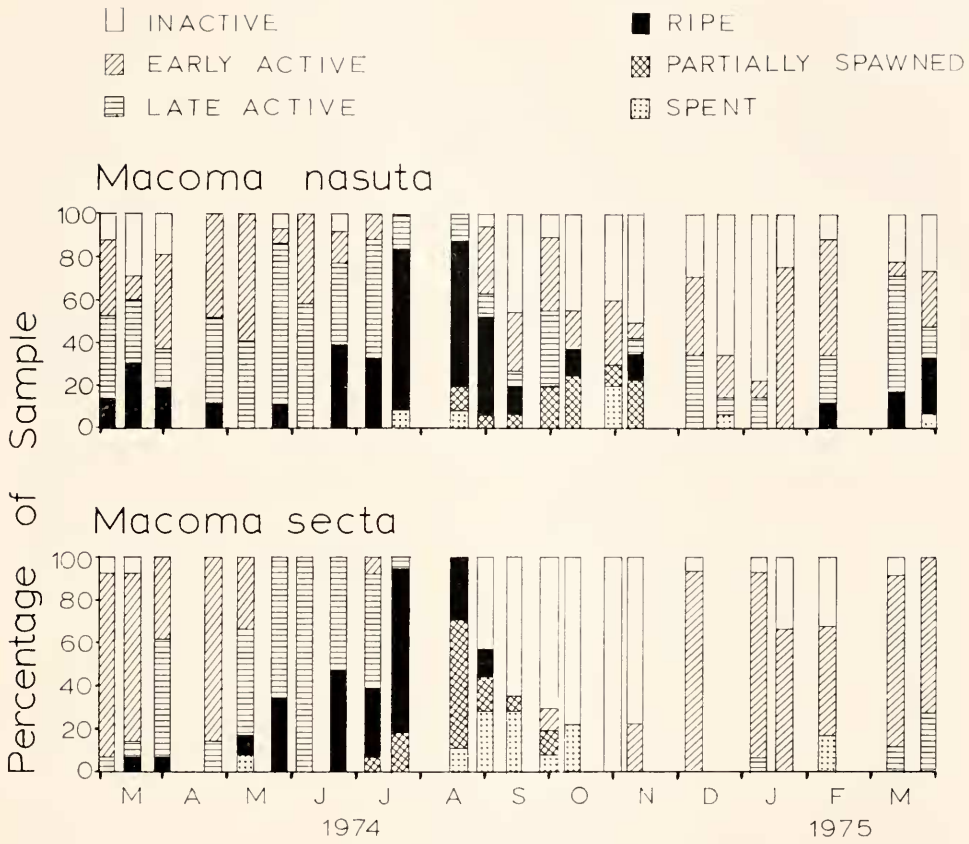

FIGURE 2. Comparison of population gonadal state of *Macoma nasuta* with *M. secta*.

very short period of time. Simultaneously, the follicle cells grow rapidly to fill the empty lumen. Frequently the new year's primary gonia begin growing within the follicle cell matrix. The small spherical cell inclusions of the females begin to appear.

Alveoli of *M. secta* initiate neither follicle cell production nor gametogenesis. Phagocytosis is sometimes in evidence.

Spent. This stage in *M. nasuta* is also shortly lived. A few residual gametes are left and follicle cells fill the alveoli. The females' spherical inclusions have grown in size and in numbers. The alveoli of *M. nasuta* remain organized and make a smooth, quick transition to the inactive state.

In *M. secta*, the alveoli have a shrunken, compressed appearance. Only a few residual gametes are left to identify sex. Phagocytosis is evident inside and outside of the alveoli, consuming pycnotic cells. Tissue is in extremely poor condition. This is a regressive stage with no cell buildup.

Gametogenic cycle

Macoma secta. Gametogenesis in *M. secta* began in November as the population entered the early active phase (Fig. 2). Gonadal development throughout the winter months was, however, very slow. Most clams remained in the early active stage until April. During this time the minimum sediment temperatures were consistently below 10° C, and the lowest seawater temperature averaged 11.0° C (Fig. 1). Besides the thermal stress, the rainy season during the winter months caused a drop in the average salinity.

As temperatures increased in April and the rainy season ended, the rate of gonad development increased and the late active phase was entered. This period was shorter and lasted approximately through June. Great numbers of sperm were found in the testes, which appeared to be fully viable, whereas very few mature oocytes were encountered; most eggs were still connected to the basal membrane of the alveolus.

Ripe clams were encountered primarily in July and early August. The definition of ripe given here may be more restrictive than previous works. However, it is to be shown that spawning occurs very rapidly for an individual, on the order of two to three weeks maximum. Those individuals considered ripe must necessarily be near completion of gametogenesis. This narrow point in the cycle was reached at the time of the highest yearly temperatures (monthly mean) which for both the seawater and sediment temperatures approximated 15.5° C.

Most spawning occurred in August. There may have been a temperature stimulus for this since average seawater and sediment temperatures began to drop toward fall readings. The discharge of gametes was accomplished quickly for the population as a whole and the spent stage was entered in late August (Fig. 2). The gonads were in a disrupted state at that time. While temperatures were still high enough for the clams to effect repair, the inactive state was very quickly entered in September. The spent stage was by far the shortest. Follicle cells began to fill the alveoli. The gonads started to reorganize, building up reserves for the early active period which started again in November.

Macoma nasuta. Although the same six stages well describe the gametogenic series in *M. nasuta*, their synchrony with time differed greatly from *M. secta.* In general, the partially spawned and spent stages were rarely encountered, owing to their extremely short duration. The remaining four stages were present in some numbers in nearly every month (Fig. 2). Exceptions were few; no clams were found in the inactive stage in July and August, early active stage in August or ripe stage in December and January. Consequently the gametogenic pattern was somewhat obscured.

Despite these problems, there did appear to be a seasonal pattern. The spring spawning schedule was as follows. From a maximum of clams in the inactive stage in December and January, the early active stage was entered in January and February. In March they rapidly entered the late active stage. Late in that month and in April, they apparently spawned as the number of ripe individuals in the samples decreased. No partially spawned clams were noticed in this series, but that was not surprising. The seemingly premature presence of spent individuals in July and August may be explained by this spring spawning, which was very

slight and, based on field observation of recruitment, may not often be successful (Rae, 1975).

The main gametogenic series occurred in the fall spawning schedule. The inactive period was left in March and gametogenesis was initiated in April and May. The clams continued gamete buildup into May and June, finally ripening in July and August. The population appeared to spawn over a wide period of time from August to November, as evidenced by the occurrence of the partially spawned state. Thereafter, the spent stage was briefly passed through and the clams became inactive. As will also be shown later, the partially spawned and spent stages were extremely short in duration and are presented here basically for continuity. Ripe individuals essentially passed to the inactive stage. Individuals probably spawned all at once, as the apparent brevity of the spawning stage indicates, however as a population, this was accomplished slowly.

It is possible that many clams stretch their gametogenic period over the spring and fall schedules. Surely there are many clams that do not fit either schedule. Also it is suspected that some spring spawners build up gametes early and simply remain ripe for a long period of time, spawning in the fall.

The correlation with temperature noticed in *M. secta* was not readily noticed for *M. nasuta*. *M. nasuta* may have a rather plastic endogenous reproductive rhythm that temperature controls in some complex way. The average temperatures found at the time of spring and fall spawning were approximately the same (about 14° C). Possibly this optimized larval survival because of the temperature itself or because of a timing factor.

Comparative gametogenesis

The results indicate distinct variation in gametogenic cycles in the genus *Macoma*. In order to view the population as a whole, the stages inactive through spent were assigned numbers 1 through 6 with a new cycle starting with 7 for inactive and continuing likewise. In this way a nonparametic mean could be assessed for the population gonadal state on each collection date (Fig. 3).

Generally *M. nasuta* developed gametes earlier in the winter than *M. secta*. However, *M. secta* constantly advanced in the cycle while *M. nasuta* remained in the active stage longer. Spawning was rapid for *M. secta* in mid-August whereas the *M. nasuta* population was slower, having spawned from mid-August through November. The graph was split during this period for *M. nasuta* because the distribution of stages was bimodal. This was because of the rapid change from the ripe to the inactive or early active state for individuals. One mean for the samples in this period would falsely indicate the nature of the population's slow progression through the spawning stages. As the mean's ranges indicate, the *M. nasuta* population was more variable as to gonadal state.

Although the two species proceeded through the gamete buildup with approximately the same timing, spawning did not appear to overlap. *M. secta* spawned in August whereas *M. nasuta* appeared to spawn slightly in May and again from September through November. This minimized the loss of gametes to cross fertilization, a distinct possibility for sympatric species.

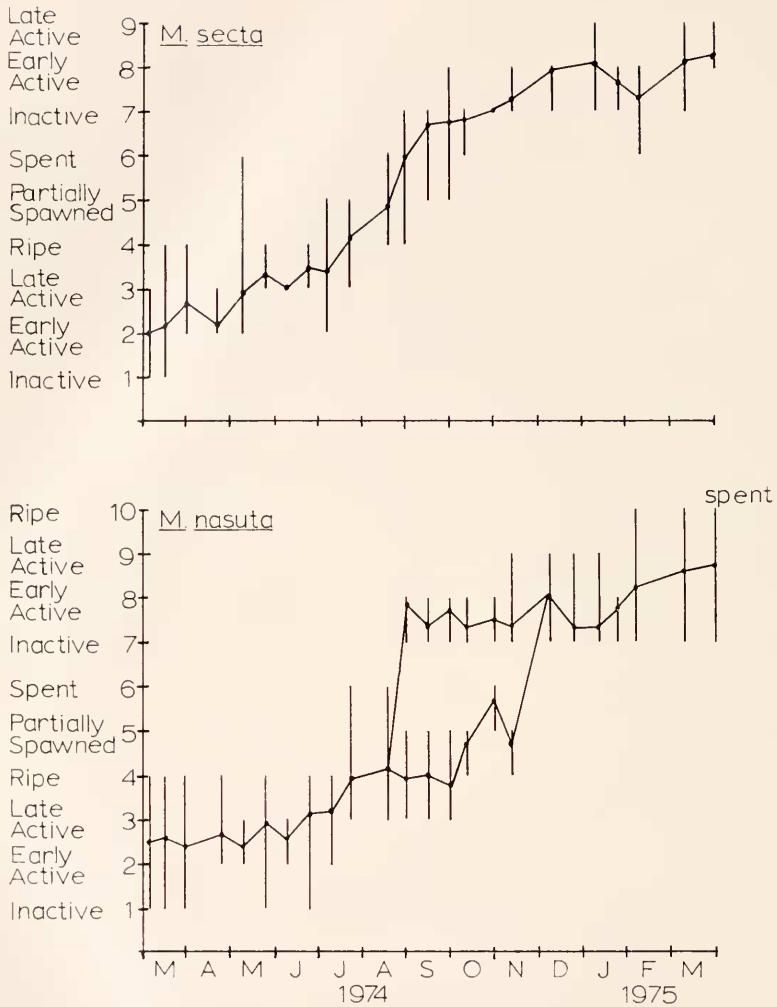

FIGURE 3. Gonadal development of *Macoma secta* and *M. nasuta* populations. Means and ranges are presented for each collection date. The ordinate represents advancing stages of gametogenesis.

Sex ratios

In this study, gonadal sections from a total of 344 individuals of *M. secta* and 336 of *M. nasuta* were examined. For *M. secta* the total sex ratio was 149 males : 138 females : 54 indeterminate. For *M. nasuta* the ratio was 150 males : 156 females : 19 indeterminate. It is difficult to determine accurate sex ratios during the inactive phase, because males often retain sperm and females rarely retain eggs. Thus, observed ratios would be biased in favor of males with many females being classed as indeterminate. To counter this bias, the sex ratio was deter-

mined by adding together only those samples wherein all specimens were sexed. Chi-square tests were performed against a 1 : 1 sex ratio. Nonsignificance was found in both cases (*M. secta* $X^2 = 0.627$, $0.5 > P > 0.1$; *M. nasuta* $X^2 = 1.10$, $0.5 > P > 0.1$). The null hypotheses of 1 : 1 sex ratios were accepted.

It is not certain whether there is sex reversal or not in *M. secta* due to the impossibility of sexing during the inactive stage. However, most of the *M. nasuta* individuals are sexable throughout that period, and no indications of sex reversal were found.

Commensals and parasites

The presence of commensals may have an effect on reproduction and certainly the presence of parasites can have a devastating effect on reproduction and population stability (Obrebski, 1975). All clams of both species were examined for commensals and parasites, both those attached to the mantle and visceral mass, and those which may have embedded in the gonad or digestive diverticula, common attack points.

Both species were found to be remarkably free from both types of pests. No commensals or parasites were found on *M. nasuta*. One specimen of *M. secta* was completely castrated by the presence of a digenetic trematode. Three specimens of *M. secta* had commensals attached to the mantle near the ctenidia. They were identified as the nemertean, *Malacobdella grossa*. Examination of the infected clams revealed completely normal gonadal development. Addicott (1952) reported the incidence of *M. grossa* commensalizing *M. secta* in Elkhorn Slough as 15.4% and for *M. nasuta* 6.0%.

Spawning

On different occasions in August, 1974, spawning of ripe animals was attempted. Various thermal and chemical methods were tried, including heat shock, cold shock, and slowly increasing water temperature in conjunction with introduction of sperm and/or egg suspension. All these attempts proved ineffectual in spawning either species. Caddy (1967) also had poor results with *M. balthica*. After repeated attempts, he succeeded in inducing only a few clams to spawn on one occasion.

Discussion

No hermaphrodites were found for either species, providing evidence that adults of both species are probably gonochoristic. Coe (1945) mentioned that out of 10,000 bivalve species, only 400 are known hermaphrodites. It is unknown whether either species is protandrous; common for gonochoristic species. Caddy (1967) indicated a strong possibility for this in *M. balthica*, while Lammens (1967) doubted protandry for the same species.

Typically in bivalves, connective tissue is found around the alveoli as well as the follicle cells within the alveoli. This has been demonstrated in *Crassostrea virginica* (Loosanoff, 1942, 1965) and *Ostrea edulis* (Loosanoff, 1962). Since this tissue disappears with the growth of alveoli, Loosanoff (1942) attributed a

nutritive function to it. However, this connective tissue is never found in either *M. secta* or *M. nasuta.* Lammens (1967) reported this also for *M. balthica.* He tested the inner follicle cells histochemically with sudan black B and obtained positive results indicating a probable nutritive function. Coe and Turner (1938) also attributed a nutritive function to these cells in *Mya arenaria* which has a similar connective tissue structure as *Macoma.* Follicle cells in *M. secta* and *M. nasuta* also seem to play an important role in alveolar nutrition.

There is a great difference in the post-spawning state between *M. secta* and *M. nasuta.* In *M. secta* as in *Mytilus edulis* (Chipperfield, 1953), the gonad disappears, only disorganized cells being left. However, for *M. nasuta,* as with *Cyprina islandica* (Loosanoff, 1953) and *Venus striatula* (Ansell, 1961), the alveoli retain their shape and fill up with the vacuolated follicle cells.

Both *M. secta* and *M. nasuta* initiated gametogenesis in late fall, but both also entered a period of dormancy during the winter months. Examination of Figure 3 suggests some gonadal regression was possible during this time for both species. The timing of this possible mid-winter resorption did correspond to the most stressful period of the year, January, when heavy Pacific storms brought much rain and cold weather. As demonstrated by Loosanoff and Davis (1952) *Crassostrea virginica* was unable to metabolize glycogen below 10° C. Minimum sediment temperatures were below this temperature during the winter. This may in part explain the observed dormancy. The range of salinities encountered (Fig. 1) increased, which produced a high environmental variability and uncertainty in osmotic stress for the clams. By comparison, the closely related *M. balthica* undergoes active gametogenesis in the winter, from September through February, in the English Channel with no dormancy whatever (Caddy, 1967).

The indications are that temperatures exogenously control spawning for bivalves. The relationship is far from simple. Temperature may optimize a species adult physiological development or optimize its larval survival as a timing mechanism. Loosanoff and Davis (1952) showed that a temperature of 15° C must be reached in order for *Crassostrea virginica* to spawn. However *C. virginica* has been shown to have physiological races which require varying temperatures above 15° C to accomplish gametogenesis and spawning (Loosanoff and Nomejko, 1951 ; Loosanoff, 1969). This subject is well reviewed by Giese (1959).

There are many variations in the timing of gametogenesis in bivalves. For populations of *M. balthica,* in the Netherlands (Lammens, 1967) and in the Thames Estuary, England (Caddy, 1967), spawning was reported in March and April. This represents an entirely different cycle, compared to *M. secta* which spawns in August and *M. nasuta* which spawns in May and from September to November. *Ostrea edulis* transplanted in Maine (Loosanoff, 1962) begins its active period in May, avoiding winter buildup entirely. In *Cyprina islandica* (Loosanoff, 1953), gametogenesis occurs principally in the late fall and early winter. There is a slow down in the winter but no dormancy, and it resumes again in spring with increasing temperatures. *Protothaca staminea* (Quayle, 1943) undergoes a short dormancy in December or January after a buildup of follicle cells. However, beginning in January and February active buildup commences despite quite low temperatures. In *Tresus capax* (Bourne and Smith, 1972) another extreme case is found wherein

gametogenesis is strong from October through January with an early spring spawn. Here the low winter temperatures of British Columbia's waters have no effect on gametogenesis.

Results (Fig. 3) indicate that *M. nasuta* spawns twice a year in Tomales Bay. In San Francisco Bay, Packard (1918) noted that because of two recruit pulses per year, reproduction of *M. nasuta* was probably semiannual. Having noticed no clear cut year classes in the size—frequency distribution of *M. nasuta*, Addicott (1952) interpreted a year-round spawning of the calm in Elkhorn Slough. Progressing south it appears *M. nasuta* may fulfill a potential of year-round spawning. Coan (1971) noted that *M. nasuta* spawned in the spring or early summer in Oregon. Possibly a threshold temperature for spawning was only reached once (the maximum). This type of behavior has been noted for *Mya arenaria*. Coe and Turner (1938) and others reported one spawning for the clam in New England waters, but Pfitzenmayer (1962) reported two separate spawnings a year further south in Chesapeake Bay. It has been shown that for populations of *Crassostrea virginica* from different geographical areas, physiological variants do occur that respond differently when subjected to conditioning at the same temperature (Loosanoff, 1969).

Rand (1973) has proposed a descriptive model on the temporal aspect of breeding strategies. The environment is represented as the complex vector of its components $e = (e_1, e_2, \ldots)$. Over time he has assigned means and variances to e representing different climates. The function of energy acquisition for both adults and larvae are different according to their physiology, abilities to acquire energy, and environmental grain (Levins, 1968). These functions are in turn dependent on e. Simulation of reproductive strategies of a hypothetical population in different climates indicated the following: northern harsh climates were characterized by a single synchronous spawning per year; temperate climates by two spawnings; and tropical by year round spawning (Rand, 1973).

Synthesis of the literature on reproductive timing of *Mya arenaria* and *Macoma nasuta* on the east and west coast of North America, respectively, indicates general agreement with Rand's (1973) model of changing reproductive strategies along a latitudinal gradient. Both bivalves exhibit a unimodal reproductive pattern in their northern harsher ranges. In their latitudinal midranges both species show a bimodal reproductive pattern. Also, *M. nasuta* apparently spawns year-round in its milder southern range.

That temporal breeding strategies depend integrally on the climate variance may be an important element in sympatric speciation for certain groups. Rand's (1973) model was based on a geographical gradient. However, the same description of breeding strategies should apply to any gradient from physically controlled to biologically accommodated climates (Sanders, 1969).

The intertidal zone provides a similar gradient proceeding from high to low tide zones. In studying the dynamics of high and low intertidal populations of the limpet, *Collisella scabra*, Sutherland (1970) found that high populations (harsh climate) spawned once a year while low populations (mild climate) spawned most of the year. This tendency is also apparent in examining the sympatric species of *Macoma*. *M. secta* (harsher climate-mid-tide) spawns once a year and *M. nasuta* (mild climate-low tide) spawns twice a year.

This work represents part of a thesis submitted in partial fulfillment for the M.S. degree at the University of the Pacific. I wish to express appreciation to all the members of my committee for use of their personal equipment and libraries, help and interest throughout my study at Pacific Marine Station; Dr. J. Blake, Chairman, and Drs. V. Loosanoff, S. Obrebski, and E. Smith, Director. Two anonymous reviewers helped in the final presentation.

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Summary

1. Spawning probably took two to three weeks for *M. secta* individuals and one to two days for *M. nasuta* individuals. Gonads of inactive *M. secta* are entirely disrupted and hardly recognizable, while gonads of *M. nasuta* remain organized and are filled with vacuolated *follicle* cells. Phagocytosis is pronounced only in spent males of *M. secta*.

2. *M. nasuta* females are characterized by noncellular spherical inclusions in *follicle* cells which are probably nutritive in function. They are numerous and large in size in the inactive stage and decrease in numbers and size as gametogenesis progresses.

3. The *M. secta* population was rather synchronous in its progression through the gametogenic stages and spawned in August. Individuals of the *M. nasuta* population were rather asynchronous in passing through the gonadal cycle; the population spawned in May and from September through November.

4. The null hypotheses of 1:1 sex ratios were accepted for both species. No hermaphrodites were found nor any evidence for sex reversal in either species.

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